Wetlands
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ORIGINAL RESEARCH

Co-occurring Mangroves and Salt Marshes Differ in Microbial Community Composition

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Abstract

Coastal ecosystems such as mangroves and salt marshes store large amounts of carbon due to high rates of plant productivity and low organic matter decomposition rates in anoxic soils. As woody mangroves continue to encroach into herbaceous salt marshes, it is important to understand how these wetland biomes differ in soil microbial communities. Mangroves and marsh plants have different rooting structures and chemical qualities and could generate different environments for soil microbes, thus leading to changes in soil carbon processing. In an ecotonal ecosystem in Florida, where mangroves are rapidly encroaching into salt marshes, we compared wetland soil microbial community composition and function in mangrove-dominated vs. salt marsh-dominated plots. Microbial community structure differed between mangrove-dominant and marsh-dominant plots. The top indicator genera in the marsh-dominated plots belonged to putatively anaerobic groups (*Tepidibacter*, *Caldithrix*, *Desulfovibro, Fibrobacteres, Thiotrichaceae*) while top indicator genera in mangrove-dominated plots had representatives within *Acidobacteria*, *Nitrospirae*, and *Proteobacteria*. In a substrate-induced respiration assay, samples from mangrove plots with the greatest root mass also had the highest rate of labile C substrate consumption. Our results suggest that mangroves and marsh plants have different sediment microbial communities and that future mangrove encroachment into salt marshes could alter soil microbial communities with potential implications for soil carbon storage.

Keywords Blue carbon · Microbial communities · Mangrove · Saltmarsh · Wetlands · Soil

Introduction

Coastal ecosystems such as mangrove forests and saltmarshes store large amounts of carbon and are thus known as "blue carbon sinks" (Chmura et al. 2003; Nellemann et al. 2009; McLeod et al. 2011). High rates of primary productivity and slow decomposition rates combine to generate high carbon sequestration in these ecosystems (McLatchey and Reddy 1998). Specifically, low soil oxygen availability decreases microbial activity in wetland soils and drives the accumulation of carbon-rich organic matter (Donato et al. 2011; McLeod et al. 2011). Increasing temperatures and rising seas threaten coastal ecosystems and are causing dramatic shifts in wetland plant community structure (Perry and Mendelssohn 2009; Osland et al. 2013; Cavanaugh et al. 2014). While we know that wetland plant communities are changing (Osland et al. 2013; Saintilan et al. 2014) and that these changes alter carbon storage (Bianchi et al. 2013; Doughty et al. 2016; Kelleway et al. 2016; Yando et al. 2016), we know little about the microorganisms responsible for organic matter decomposition in wetland soils dominated by different plant types (but, see Rietl et al. 2016).

Microbial community composition can affect decomposition (Allison et al. 2013) and nutrient cycling (Reed and Martiny 2013) in soils. Life history strategies and phylogenetic grouping of microorganisms can influence soil C-cycling rates and the thus the fate of soil C (Schimel and Schaeffer 2012). In coastal wetland ecosystems, changes in soil microbial community composition are often tightly linked with changes in ecosystem functions, (e.g. Morrissey and Franklin 2015a, b) suggesting that these communities may

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influence ecosystem response to global change. Because coastal wetland ecosystems are important for carbon storage and storm surge protection, an understanding of microbial community dynamics in wetland soils is urgently needed.

Increased temperatures and sea level rise have contributed to the expansion of mangrove forests into saltmarshes (Osland et al. 2013; Cavanaugh et al. 2014; Saintilan et al. 2014; Giri and Long 2016). In the Eastern United States, this climate-driven woody plant expansion into herbaceous wetlands has been attributed to a decline in severe freeze events (days colder than −4°C) (Cavanaugh et al. 2014). Sea level rise is also contributing to this expansion by opening up new waterways that allow mangrove propagules to disperse upstream easily (Krauss et al. 2011) At one site in Florida, we have shown that mangroves have increased in abundance by 69% over the past 7 years, thus increasing ecosystem C storage by 22% (Doughty et al. 2016). The soil environment associated with mangroves and marshes differs (Doughty et al. 2016; Coldren et al. 2016) but little is known about the soil biota that inhabit each of these primarily anoxic environments (Chambers et al. 2016). As many other marsh sites around the world are also undergoing mangrove encroachment (Saintilan et al. 2014; Yando et al. 2016), understanding differences between soil microbial communities associated with mangroves and marshes in this transitional state may be important for understanding changes in soil carbon processing.

The anoxic conditions in saturated marsh and mangrove soils permit organic matter accumulation, enabling wetland soils to build vertically and keep up with sea level rise (Middleton and McKee 2001; Neubauer 2008). However, roots and other structures of wetland plant species deliver oxygen to soils via aerenchyma, and thus vegetation shifts affecting dominant root morphology can potentially increase oxygen availability in soils (McKee et al. 1988; Jackson and Armstrong 1999; Armstrong et al. 2000; Reddy and DeLaune 2008). Woody plant roots, like mangroves, have different chemical qualities (Perry and Mendelssohn 2009) and physiological characteristics (Skelton and Allaway 1996; Purnobasuki and Suzuki 2004) than herbaceous plant roots and could deliver different amounts of root exudates (Bertin et al. 2003). Root-mediated changes in the soil environment could provide soil microorganisms with oxygen or other substrates, potentially altering microbial community structure (Noll et al. 2005; Lipson et al. 2015) and fueling more organic matter decomposition leading to decreases in soil C (Freeman et al. 2001; Wolf et al. 2007). Thus, assessing the differences in wetland soil bacteria under mangroves vs. marshes may allow us to better understand soil organic matter processing as mangroves continue to encroach into marshes.

Here we aimed to examine variation in microbial community composition and function in mangrove and marsh dominated soils. This was accomplished in an ecotonal ecosystem in Florida where we have been documenting the ecosystem impacts of mangrove encroachment into salt marshes (Simpson et al. 2013; Doughty et al. 2016; Coldren et al. 2016). Specifically, we investigated bacterial community composition in soils from plots dominated by either mangroves or marshes and positioned across a mangrove-marsh ecotone. Using incubation experiments, we assessed wetland soil respiration in response to labile substrate and oxygen availability. We hypothesized that (i) mangrove-dominated vs. marsh-dominated plots would have distinct microbial community structures, (ii) soil organisms from mangrove-dominant plots will respire more CO_2 in response to labile substrates and (iii) mangrove-dominant plots would have higher microbial CO_2 respiration rates than marsh-dominant plots in both aerobic and anaerobic conditions.

Materials and Methods

Site Description

We conducted this research at the Kennedy Space Center (KSC) and the overlying Merritt Island National Wildlife Refuge (MINWR), on the Eastern Coast of Florida (28.4889°N, 80.5778°W). Coastal wetlands in this area, and many areas in Florida, were impounded, or "ditched", in the 1950s in order to control for mosquito populations. The study site we used is tidally connected to the Indian River Lagoon through a series of culverts that are currently unmanaged and remain open to allow natural tidal flow. The tides within the IRL are microtidal and vary from 0.1 to 0.7 m (Smith 1987) and the soils consist of organic matter and/or silty clays over sand and irregularly stratified mixed sand and shell. Soil salinity ranges from 30.0 to 50.8 ppt.

Though mangroves have been abundant in this region in the past, over the last five decades, this site has undergone many rapid vegetation changes due to freeze events, which can kill off mangroves (Provancha et al. 1986). However, the recent absence of severe freeze events at this site has allowed mangroves to increase dramatically. In the last 7 years alone, mangrove abundance has increased by 69% at MINWR (Doughty et al. 2016). The co-dominance of these two species makes MINWR an ideal location to compare mangrove and marsh soil communities (Coldren et al. 2016). Specifically, the mangrove-marsh ecotone at this site is dominated by three mangrove species (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa)* and four marsh species (*Spartina alterniflora*, *Distichlis spicata*, *Batis maritima* and *Salicornia bigelovii*). *A. germinans* and *L. racemosa* are the dominant mangroves at our site and *D. spicata* covers 85% of the marsh plots at our focal site.

Experimental Design

In 2013, we established a series of ten 3 m × 7 m transects at our site that spanned the transition from mangrove-dominated to salt marsh grass-dominated vegetation. We randomly selected two $1m^2$ plots at either end of these transects, one of which was dominated by small white mangroves (>70% of plot cover where young mangroves were encroaching into marshes) and one of which was dominated by the marsh grass *D. spicata* (>90% of plot cover). From hereafter we refer to these plots as either "mangrove-dominant" and "marsh-dominant" and we characterize the two different plot types as "vegetation types" (grass vs. tree; Fig. 1). We chose transects with small younger mangroves, rather than mature larger mangroves, in order to examine soils from plots in the transitional state when mangroves have recently encroached into marshes. Using a combination of sequential aerial photos and growth indices from a previous study, we were able to identify the focal mangroves in mangrove-dominant plots as juvenile trees (Doughty et al. 2016). Though these transects are rather short, the mangrove-dominant and marsh-dominant plots at either end represent distinct vegetation types and yet do not differ in other state factors that could change the microbial community. Thus, we are able to control for abiotic factors such as salinity, organic matter depth of soils, surface elevation, percent carbon, etc. (Table 1) that have either been shown to or would likely influence wetland soil microbial communities (e.g. Morrissey et al. 2014; Morrissey and Franklin 2015a).

We investigated wetland plant influence on soil communities and respiration by sampling soils from the above-described $1m^2$ mangrove-dominant and marsh-dominant plots (two vegetation types × 10 plots; <7 m away) that were similar in other environmental conditions (Table 1). We also sampled soils from three randomly chosen pure mangrove and pure marsh plots outside these transects to compare microbial substrate induced respiration (SIR) in these pure vegetation types with the ecotonal plots (Fig. 1). The SIR assay is the only analysis that utilized the pure mangrove and pure marsh samples but we report root and soil characteristics of these plots in Table 1.

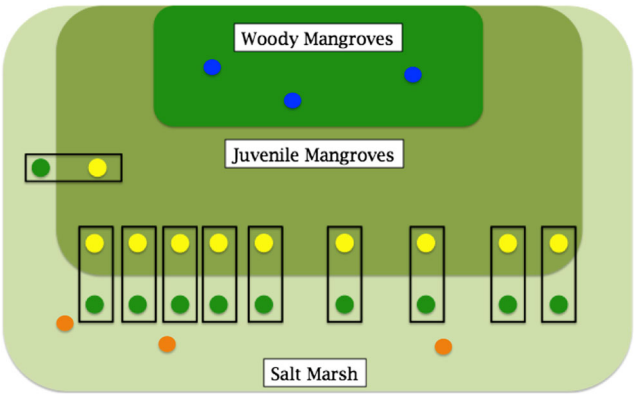

Fig. 1 Experimental Design set up. Plots were set up across the mangrove-marsh ecotone, where there were a mangrove-dominant plots (>70% cover, yellow dots), and marsh-dominant plots (>90% cover, green dots). Three random samples were taken in the "pure mangrove" area, represented by blue dots, and three random samples were taken in the "pure marsh" area, represented by orange dots. Picture is not to scale

Environmental Analyses

Root Biomass

In October 2014, a year after the mangrove- and marsh-dominant plots were established, soil cores were taken to obtain belowground root biomass at three depths. One soil cores was taken in each of the 20 plots under the dominant species (10 mangrove-dominant plots-*L. racemosa*, 10 marsh-dominant plots- *D. spicata*) to a depth of 60 cm using a stainless steel gouge auger (AMS sampling, American Falls, ID) and sectioned into 0–20 cm, 20–40 cm, and 40–60 cm increments. After washing through a 2 mm sieve, roots were sorted into fine (< 2 mm) and coarse (> 2 mm) diameter categories, as well as live and dead. After drying the roots in an oven, total dry root mass was assessed. We used total root mass because we wanted to characterize the root organic matter change during this interval. In March 2016, in order to observe the change in root mass over time, root mass was again assessed by following the above-described coring and sorting procedures. Root biomass was also obtained in 2016 for the pure mangrove and pure marsh plots ($n = 3$).

Soil Characteristics

Soil salinity was measured in the field using a Refractometer (Extech, Model RF20). Oxygen measurements were taken in the field using a Fire Sting O_2 Optimal Oxygen Meter (Pyroscience, Bremen, Germany) in mangrove-dominant and marsh-dominant plots at depths of 10 and 40 cm in March 2016. A portion of each soil core was dried for measurement of moisture (dried for 24 h at 70 °C) and carbon (C) concentration (Leco TruSpec CN, St. Joseph, MI). Carbon was measured at depths of 5, 10, 15, and 20 cm.

Soil Microbial Community Analyses

For molecular analysis we took 2 cm × 5 cm subcores horizontally at 10 cm from the previously described 60 cm soil cores (1 core per plot) and immediately placed them on dry ice in the field. Upon return to the laboratory, samples were stored at −80 °C.Though recent studies have shown that soil fungi are abundant in salt marsh ecosystems (Kandalepas et al. 2010; Rietl et al. 2016), we chose to focus our study on the soil prokaryotes. Whole community bacterial DNA was

Table 1 Mean ± SE of environmental soil parameters for each vegetation type

Vegetation type	Organic layer	Root biomass–g	%C	Surface elevation	Oxygen	Salinity
Marsh-dominant	8.8 cm ± 2.2	3.2675 ± 1.2	4.3531 ± 3.1	246.3 mm ± 16.11	Below Detection	20–50 ppt
Mangrove-dominant	8.0 cm ± 1.4	1.9776 ± 0.7	4.0833 ± 2.5	254.4 mm ± 13.97	Below Detection	20–50 ppt
Pure marsh	7 cm	2.9800 ± 1.2	7.2196 ± 0.8	NA	Below Detection	20–50 ppt
Pure mangrove	11 cm	12.290 ± 1.2	10.593 ± 1.3	NA	Below Detection	20–50 ppt

Porewater oxygen, %C, and salinity were taken to a depth of 20 cm

extracted from ~0.5 g of each of the soil subcores using MOBIO PowerSoil DNA Isolation Kit (MOBIO, Carlsbad, CA). To increase DNA yield, modifications were made to the protocol. Specifically, samples were centrifuged for 2 min at 10,000×*g* before extractions to pellet the cells and eliminate added liquid. Samples were extracted in duplicate and pooled together prior to DNA elution (Step 14 of the kit). DNA purity and concentration were analyzed using the Qubit Flurometric Quantitation 3.0 (Qubit Company, New York, NY) and stored at −20 °C until sequencing. DNA extracts were verified using agarose gel (1%) electrophoresis and ethidium bromide staining prior to shipping for sequencing. Samples were sent to GENEWIZ (South Plainfield, New Jersey) for library preparations and Illumina MiSeq sequencing of the V3, V4, and V5 hypervariable regions of prokaryotic 16S rDNA as described in (Wu et al. 2017). Analysis followed the GENEWIZ 16SMetaVx pipeline. Two amplifications were preformed, in the first GENEWIZ amplified the V3 and V4 regions with primers containing the following target sequences: CCTACGGRRBGCASCAGKVRVGAAT and GGACTACNVGGGTWTCTAATCC. In the second, GENEWIZ amplified the V4 and V5 regions with primers containing the following target sequences: GTGYCAGCMGCCGCGGTAA and CTTGTGCG GKCCCCCGY (Wu et al. 2017). Indices were attached to PCR products and the normalized libraries were then multiplexed and subjected to sequencing on an Illumina MiSeq (Illumina, San Diego, CA, USA). Some samples sent for sequencing failed, either because there was not enough extractable DNA or because the quality of this DNA was poor in those soils. As the soils at MINWR are very sandy, it is possible that we did not have enough organic matter to be able to extract sufficient DNA. Because of these challenges, only 4 mangrove-dominant soils and 6 marsh-dominant soils were successfully sequenced.

Substrate Induced Respiration

We used one soil core from each plot (10 each of marsh-dominant and mangrove- dominant and 3 each of pure marsh and mangrove) taken in March 2016 to examine soil respiration as a measure of microbial function. We estimated relative aerobic substrate induced respiration from soil cores using the substrate-induced respiration (SIR) method described in Fierer et al. (2003). We employed this method to determine the potential ability of mangrove- dominated vs. marsh-dominated soil microbial communities to process labile substrates in aerobic conditions. Briefly, 10 g of wet soil from the mangrove-dominant, marsh-dominant, pure mangrove, and pure marsh samples were weighed into individual 55 ml glass vials with 10 ml of yeast extract (Difco Laboratories, Detroit, MI) solution. The glass vials were sealed with rubber septa and placed on a shaker for the duration of the 4 h incubation. Cumulative CO_2 concentrations were measured in each vial at times 0, 45 min, 1 h 15 min, 2 h, and 2 h 45 min. Measurements were taken using an infrared gas analyzer (Licor Model LI-7000, Lincoln, NE), and rates were calculated as μg C-CO_2 g soil^{-1} h^{-1}.

Soil Incubations

We performed soil incubations in both anaerobic and aerobic conditions in order to examine potential CO_2 efflux of the soils from mangrove-dominated and marsh-dominated plots We used one soil core from each plot to perform the incubations (2 vegetation types × 10 plots × 2 oxygen treatments). The oxygen treatments were included to assess how microbial function, soil respiration, changes across vegetation type (mangrove dominant and marsh dominant) under different oxygen conditions. We sieved subsamples of soil (~5 g wet weight) from each large core and incubated at room temperature in oxic and anoxic conditions for a duration of 68 days. Soil was weighed into 55 ml glass vials (Wheaton Serum Vials, Millville, NJ) and sealed with rubber septa and metal seals. Vials were flushed with CO_2-Free Air at the start of the incubation and an additional 2 times throughout the incubation, for 5 min each time. Cumulative CO_2 measurements were measured in each vial on days 1, 2, 4, 6, 13, 20, 21, 23, 28, 35, 42, 49, 50, 52, 56, 63, and 68. Measurements were taken using an infrared gas analyzer (Licor Model LI-7000). Average respiration rates (μg C-CO_2 g soil^{-1} h^{-1}) were determined for each vegetation category under oxic and anoxic conditions.

Data Analysis

Wetland plant root mass (g/m^2) and %C data were compared between mangrove-dominant and marsh-dominant plots at each depth with a one-way ANOVA with block and treatment as factors. Root mass or %C data for pure mangrove and pure marsh plots were not compared statistically with the mangrove-dominant and marsh-dominant plots due to unequal replication. When block was not significant, it was removed from the analyses. Root biomass data were log transformed prior to ANOVA due to non-normality.

Bacterial and Archaeal 16S rRNA gene sequences were processed with QIIME 1.9.0 (Caporaso et al. 2010a) using default parameters. Sequences were clustered into operational taxonomic units (OTU) by 97% sequence identity using uclust against the Greengenes database version 13_8 (Edgar 2010; McDonald et al. 2012). The sequences for corresponding OTUs were aligned using PyNAST algorithm (Caporaso et al. 2010b), which produced taxonomic assignment with RDP classifier (Wang et al. 2007). Prior to downstream analysis, OTUs accounting for less than 0.005% of sequences were removed (Bokulich et al. 2013). Samples were rarified at 168,086 reads per sample. Community composition of soils was visualized using a principal coordinates analysis (PCoA) and analyzed via a permutational multivariate analysis of variance (PerMANOVA) with the vegan package in R (version 3.2.3). Prokaryotic alpha diversity was determined using Chao 1 phylogenetic diversity index, (QIIME output). A t-test was done to determine the differences in alpha diversity based on vegetation type. To further understand how the communities differed, an indicator species analysis was performed at the genus level using R (version 3.2.3).

To gain insight into why vegetation caused differences in microbial community structure we examined bacterial groups in more detail. Previous studies have shown that root environments can be different in oxygen availability (Sorrell and Armstrong 1994), and we found that oxygen had large impacts on microbial respiration from our lab incubations. Thus, bacterial phyla identified in our study were putatively classified as aerobic or anaerobic based on an extensive literature search. We emphasize that we perform these classifications to merely explore the bacterial community changes and generate hypotheses for future work, not to definitively prove effects on vegetation on soil oxygen delivery or community composition. In order to be called "putatively aerobic" or "putatively anaerobic" a taxonomic group had to be described in the literature as either obligate aerobic or obligate anaerobic, or predominantly aerobic or predominantly anaerobic to be included in the analysis. Bacterial groups that did not fit these criteria were excluded. Supplemental Table 4 provides a complete listing of the putatively aerobic and anaerobic groups that we used. It is important to note that we do not yet know the metabolisms of all members of these microbial groups, due to the paucity of data on soil microbial metabolism, particularly for wetland soils. The relative abundances of relevant putative aerobic and anaerobic microbial phyla in mangrove-dominant vs. marsh-dominant plots was also analyzed via PerMANOVA. The relative abundance of all putative anaerobic and aerobic microorganisms (all groups were added together) were compared for both mangrove-dominant and marsh-dominant plots using a one-way ANOVA for each vegetation type. The relative abundance of relevant taxonomic groups were assessed using a one-way ANOVA with vegetation type as the main effect and Tukey's HSD for *post hoc* comparisons.

We assessed labile substrate usage in the two vegetation type soils by calculating the slopes of linear functions fitted to the carbon dioxide respiration rates (μg per g C $hr.^{-1}$) of each sample over the 4 h incubation. Concentrations of CO_2 increased linearly over time ($R^2 = 0.57–0.97$). We examined the impact of mangrove cover on SIR rates using a bivariate correlation analysis. The effects of oxygen and vegetation on CO_2 respiration for the lab incubation were analyzed using a repeated measures ANOVA (JMP 12.0, SAS Software 2012). The cumulative amount of carbon respired was determined by integrating values under the curve of the 68 day sampling period. The impacts of vegetation and oxygen on cumulative carbon respired during the 68 day incubation were analyzed using a two-way ANOVA with oxygen treatment and vegetation as factors. For statistical significance we assumed an α level of 0.05. Normality was assessed using the Shapiro-Wilks test. Data were log-transformed to conform to assumptions of homoscedasticity. Data analyses were performed using JMP 12.0 (SAS Software 2012) and R studio (version 3.2.3).

Results

Root Biomass and Soil Characteristics

In all plots, root mass was greatest in the shallow depth (0–20) and declined with depth ($p < 0.001$, Supplementary Table 1). There was significantly more shallow depth root biomass in marsh-dominant plots than in mangrove-dominant plots ($p = 0.008$). There was significantly more shallow depth root biomass in pure mangrove plots than in pure marsh plots ($p = 0.016$). Percent C was greatest in all of the plots at the 10 cm depth and did not differ due to vegetation (Table 1). Soil salinity ranged from 20 to 50 ppt at this site and did not differ in mangrove-dominant vs. marsh-dominant plots. Porewater oxygen was not detectable (readings were zero) in both mangrove-dominant and marsh-dominant subplots.

Soil Prokaryotic Community

All soils that were sequenced were dominated by *Proteobacteria* (34–44% of relative abundance of 16S rRNA

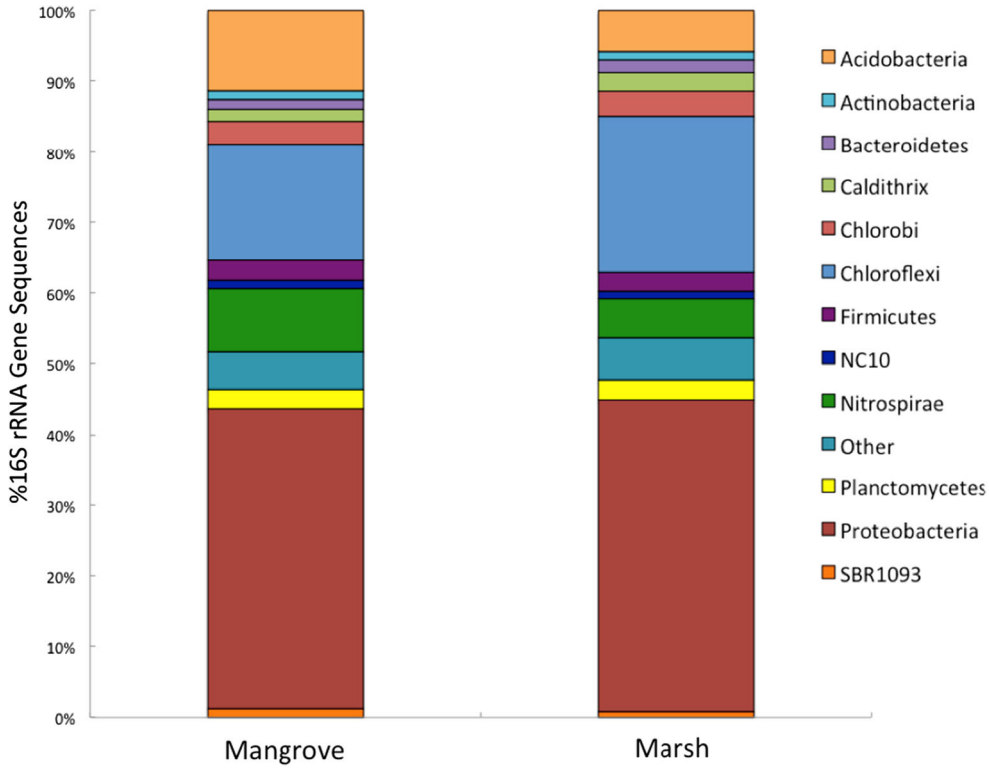

Fig. 2 Stacked bar graph of prokaryotic community composition in mangrove-dominant and marsh-dominant soilsRelative abundance of phyla (%) are reported alphabetically

gene sequences), *Firmicutes* (12–18%), *Chloroflexi* (4–6%), *Bacteroidetes* (1–2%), and *Acidobacteria* (1–4%) (Fig. 2). Marsh soils had greater prokaryotic diversity than mangrove soils (Chao1 mean±S.E., Marsh = 2332±34, Mangrove = 2275±21; $t = 2.93$, $p = 0.019$). Microbial community composition was significantly different between vegetation type as determined by a one-way PerMANOVA ($F = 1.53$, $p = 0.048$, Fig. 3). To better understand how these communities differed we performed an indicator species analysis (Table 2). The top indicator genus in the marsh ecosystem was *Tepidibacter* (class *Clostria*). Isolates from this genus have been characterized as anaerobic and fermentative (Slobodkin et al. 2003; Urios et al. 2004; Tan et al. 2012). The marsh also favored *Desulfovibrio* a genus of anaerobic sulfate reducing bacteria (Heidelberg et al. 2004; Meyer et al. 2013). The remaining indicator genera were unclassified groups within *Thiothrichaeaea* (a family of *Gammaproteobacteria*) as well as the under described phyla *Fibrobacteres* and *Caldithrix*. The top indicator genera for the mangrove soils included two genera within *Nitrospirae*, an unknown genus within *Nitrospirales* and BD2.6 within *Thermodesulfovibrionaceae*. The other indicators included unknown genera within *Acidobacteria*, *Alteromonadales*, and *Entoeonellaceae*.

Substrate-Induced Respiration

Substrate induced respiration rates were highest in pure mangrove plots as determined by a bivariate correlation analysis ($R^2 = 0.18$, $p = 0.037$). Cumulative C respired over the 4 h incubation did not significantly differ between any of the soil types but similar to the SIR rate, cumulative carbon respired tended to be highest in the pure mangrove (28.40 ± 2.31 μg per g C $hr.^{-1}$) and lowest in the pure marsh (18.27 ± 1.24 μg per g C $hr.^{-1}$).

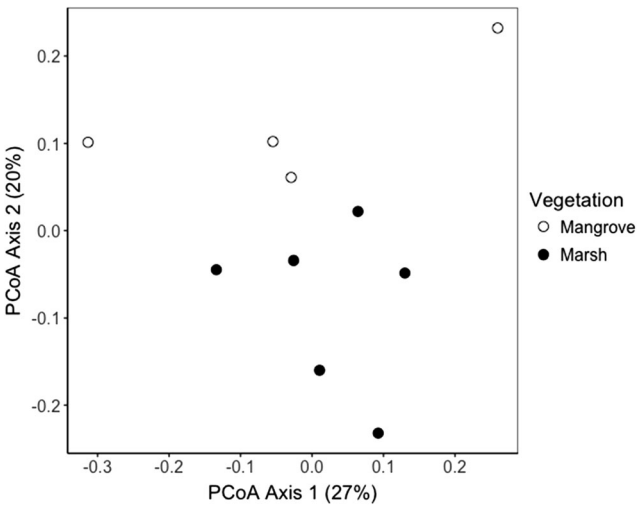

Fig. 3 Principle coordinates analysis (PCoA) comparing microbial community composition between mangrove-dominant and marsh-dominant plotsStatistical significance was evaluated by PerMANOVA. Communities were significantly different across vegetation types ($p = 0.048$)

Table 2 Five best prokaryotic indicator genera for the Marsh and Mangrove dominant soils

	Genera	Indicator value	p	Relative abundance (%)	
				Mangrove	Marsh
Marsh	Unknown genus in phylum Fibrobacteres	1	0.007	ND[a]	0.0312 ± 0.0603
	Tepidibacter (class *Clostridia*)	1	0.002	ND[a]	0.0009 ± 0.0008
	Unknown genus in phylum *Caldithrix*	1	0.005	ND[a]	0.0045 ± 0.0038
	Unknown genus in family *Thiotrichaceae*	0.99	0.024	0.0004 ± 0.0006	0.0840 ± 0.1741
	Desulfovibrio (class *Deltaproteobacteria*)	0.98	0.016	0.0003 ± 0.0004	0.0191 ± 0.0253
Mangrove	Unknown genus in order *Nitrospirales*	0.98	0.042	0.1140 ± 0.2049	0.0027 ± 0.0034
	BD2.6 in family *Thermodesulfovibrionaceae*	0.92	0.048	1.0514 ± 1.5922	0.0967 ± 0.0444
	Unknown genus in phylum *Acidobacteria*	0.85	0.004	0.3860 ± 0.1869	0.0704 ± 0.0223
	Unknown genus order *Alteromonadales*	0.84	0.034	0.0069 ± 0.0025	0.0013 ± 0.0022
	Unknown genus *Entotheonellaceae*	0.79	0.006	0.4898 ± 0.3977	0.1333 ± 0.0235

Indicator value, *p*-value, and relative abundance (mean ± the standard deviation % 16S rRNA gene sequences) are reported

[a] Genus was not detected (ND) in the mangrove soils

Aerobic and Anaerobic Soil Respiration

There was a significant effect of oxygen ($p = 0.026$) on soil respiration rate but no effect of vegetation and no significant interaction between vegetation and oxygen (Supplementary Table 2). We also found that oxic microcosms had significantly higher cumulative C respired ($p < 0.001$) but there was no interaction between vegetation and oxygen treatment (Fig. 4, Supplementary Table 3).

Discussion

We hypothesized that mangrove-dominated vs. marsh-dominated plots would have different microbial community structures and our findings support this hypothesis. Prior studies have shown that an increase or decrease in aboveground biomass (Callaway et al. 2004; Strickland et al. 2009) or changes in soil organic matter (Morrissey et al. 2014) can alter microbial community structure in wetland soils. Rietl et al. (2016) found that microbial community structure differed in salt marsh sediments with different vegetation types, particularly between *Juncus roemerianus* and *Spartina alterniflora* Similarly, we found that plots dominated by different wetland plant species (*L. racemosa* and *D. spicata*) had different microbial communities..

The change in microbial community composition we observed could be due to differences in root environment driven by the dominance of mangroves vs. marshes, which include differences in root exudates or oxygen availability. Beyond an increase in root mass in marsh soils, there was little detectable difference in the environmental characteristics of marsh- vs. mangrove-dominant soils (Table 1). Pure mangrove soils did show higher root biomass than the other plot types but this investment in prolific roots may not be added until pioneer mangroves reach maturity. However, root biomass alone may not be a good indicator of root environment changes in wetland soils because root mass does not necessarily correlate with physiological activities (exudation, nutrient update, etc.) Further, the root architecture of mangrove vs. marsh roots differ, particularly in the abundance of the oxygen provisioning tissue, aerenchyma (Skelton and Allaway 1996; Purnobasuki and Suzuki 2004). We did not measure root exudates and could not detect oxygen in the field via *in situ* measurements. This is a common problem,; porewater oxygen is often undetectable in wetland soils likely because microorganisms are consuming oxygen as quickly as it is being released, making levels of oxygen difficult to detect with field instruments (Reddy et al. 1980; Sorrell and Armstrong 1994; Armstrong et al. 2000). Redox measurements could have provided more integrated measurements of oxygen availability but this method was unavailable to us for this study. Consequently, there could be biologically relevant, yet

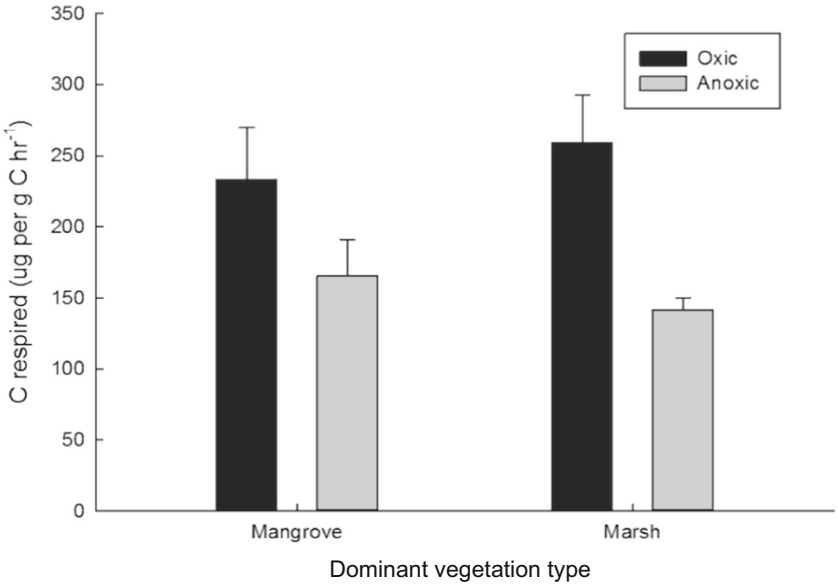

Fig. 4 Mean ± standard error of carbon respired over a 68 day soil incubationMangrove-dominant and marsh-dominant soils were incubated in anoxic and oxic conditions. Statistical significance was evaluated using a two-way ANOVA. There was an effect of oxygen ($p < 0.001$) but no effect of vegetation or interaction between oxygen and vegetation

undetectable, differences in oxygen efflux between the vegetation types capable of altering microbial community structure and function.

The top five indicator taxa were predominately anaerobic in the marsh and aerobic in the mangrove dominated plots suggesting that differences in oxygen availability between vegetation types may be influencing microbial community composition. All of the indicator taxa within the marsh dominated plots belonged to taxonomic groups containing anaerobic representatives. *Tepidibacter* and *Desulfovibrio* are relatively well described anaerobic genera typified by fermentative and metal reducing metabolism respectively (Heidelberg et al. 2004; Meyer et al. 2013; Slobodkin et al. 2003; Urios et al. 2004; Tan et al. 2012). Although less well described, members of *Calditrix (*Miroshnichenko et al. 2003, 2010; Alauzet and Jumas-Bilak 2014)*, Thiotrichaceae* (Girnth et al. 2011; Schulz 2006) and *Fibrobacteres* (Hongoh et al. 2006; Ransom-Jones et al. 2012) have been found to possess anaerobic metabolism and inhabit anaerobic environments. Phylogenetic and genomic analysis of *Fibrobacteres* has identified anaerobic metabolism as a unifying feature of the phylum (Rahman et al. 2016). In contrast, over half of the indicator taxa within mangrove dominated soils belonged to taxonomic groups containing aerobic representatives. The *Nitrospirales* order is best known for aerobic nitrifying bacteria (Lücker et al. 2010; Daims et al. 2015) and most isolates of Acidobacteria are aerobic heterotrophs (see review by Ward et al. 2009). *Alteromonadales* have previously been document to inhabit mangrove soils (Dos Santos et al. 2011) and isolates include aerobic marine bacteria (Raguenes et al. 1996; Methé et al. 2005). Little is known about *Entotheonellaceae* (Schmidt et al. 2000; Brück et al. 2008), and *Thermodesulfovibrionaceae* (Sonne-Hansen and Ahring 1999; Haouari et al. 2008) in soil because characterized members of these groups come from marine sponges and host springs respectively.

To further explore the possibility that oxygen availability could be driving the differences in community composition between vegetation types, we used a literature-based examination of the microbial groups present in our soil samples and classified taxonomic groups as putatively aerobic or anaerobic (Supplementary Table 4). Overall, communities of putative aerobic and anaerobic microorganisms were significantly different across vegetation types as determined by a PerMANOVA (Supplementary Fig. 1). These community changes show a trend of greater relative abundance of putative aerobic microbes in mangrove-dominant plots and relatively more putative anaerobic organisms in marsh-dominant plots. Though the cumulative relative abundances of aerobic and anaerobic groups did not differ due to vegetation type, the relative abundance of *Chloroflexi* was significantly greater in the marsh-dominant plots ($F = 12.93$, $p = 0.037$). Similarly, *Acidobacteria*, putative aerobes, had significantly greater relative abundance in the mangrove-dominant plots ($F = 13.20$, $p = 0.036$). We also found a higher relative abundance of the putatively aerobic phyla *Actinobacteria, Bacilli, and Nitrospira,* in mangrove-dominant plots (Nazina et al. 2001; Saarela et al. 2004, Ward et al. 2009; Yarwood et al. 2013).

Overall the indicator taxa analysis and the relative abundances of bacteria phyla suggest that mangroves could be releasing more oxygen into the soil and increasing the abundance of aerobic microorganisms. However, the metabolic potential of many taxonomic groups, is not well characterized or constrained. Consequently, future work is needed to validate the trends observed here and definitively demonstrate the influence on vegetation type oxygen delivery to soil microorganisms.

This understanding is needed because if aerobic microorganisms are able to process organic matter more quickly, as would be expected because aerobic respiration using oxygen is thermodynamically more favorable than anaerobic respiration (using alternative terminal electron acceptors), this community shift could potentially alter blue carbon storage. In another investigation of mangrove vs. marsh soil processes, Perry and Mendelssohn (2009) found that mangrove soils had slightly higher redox potential but that under these young mangroves, soil carbon had not yet changed. Similarly, we didn't find differences in soil C under mangroves vs. marshes at a landscape-scale study at this site (Doughty et al. 2016). We predict that soil C differences, if they occur due to plant-specific differences in soil oxygenation and microbial processing of organic matter, may take decades to manifest.

To examine how marsh vs. mangrove dominance may impact potential microbial carbon processing activity, we measured SIR, which allowed us to examine the abundance and potential ability of microbes to utilize a carbon substrate in fully oxic conditions (Fierer et al. 2003). We hypothesized that mangrove-dominant plots would produce more CO_2 when exposed to labile substrates due to more abundant putatively aerobic organisms. However, we found that only soils with 100% mangrove cover (pure mangrove plots) had the highest substrate-induced respiration rates. This finding supports the idea that the microbial communities associated with mangrove roots are more efficient than marsh microbes at utilizing a carbon substrate in oxic conditions. It may be that the soils of mangrove-dominant plots were not yet dominated by mangrove roots. However, we weren't able to test this idea because we couldn't discern the difference between mangrove and marsh roots in soil cores. Because we know that more oxygen can fuel microbial organic matter decomposition (Freeman et al. 2001; Wolf et al. 2007), it's possible that continuing mangrove encroachment into marshes could lead to soil carbon losses. However, increasing root biomass due to mangrove encroachment could potentially offset these decreases in soil carbon over the long-term (Doughty et al. 2016).

To determine how marsh and mangrove soil microbial respiration responds to oxygen availability, we performed a soil incubation of each soil type in oxic vs. anoxic conditions. As expected, our results indicate that microbial respiration of both mangrove and marsh soils were much higher in oxic conditions. However, counter to our hypothesis, soil CO_2 respiration was not influenced by mangrove or marsh dominance in the plots. Respiration in these incubations was likely to be influenced by microbial community efficiency and abundance, and by soil carbon availability. Consequently, differences in the chemical quality in the soil carbon pools, for instance more labile C accumulation in the marsh dominant soils, could mask differences in microbial community efficiency and abundance, generating no net effect of vegetation on soil respiration. It is important to note that we conservatively sampled soil from mangrove plots with smaller, young mangroves (Fig. 1, "Juvenile mangroves") as opposed to the larger, more mature mangrove plots where we know there is more soil C stored, more root production (data not shown), and perhaps more putatively aerobic microorganisms. Though vegetation type does not influence soil respiration in this incubation, the incubation necessarily lacked roots, which we predict are the conduits of limiting oxygen into these soils. These incubation data help confirm that oxygen is a major limitation on CO_2 efflux in these wetland soils.

Blue carbon- rich ecosystems such as mangroves and saltmarshes are exceedingly important in combatting climate change, as they store large amounts of carbon (McLeod et al. 2011). While some studies, including our own, have shown increases in aboveground C storage with mangrove encroachment into marshes (Doughty et al. 2016; Kelleway et al. 2016; Yando et al. 2016), little work has been done on belowground organisms that may regulate carbon loss from these systems. Our work provides a comprehensive assessment of microbial community structure in wetland soils where vegetation is shifting rapidly and serves as a starting point for further research into wetland soil microbial communities as dominant plant species shift with climate change. Further, we provide important insights into belowground C dynamics at a site where mangroves are encroaching into saltmarshes. Further study into wetland organic matter decomposition and the organisms that regulate this carbon processing is important to understanding wetland carbon budgets and their capacity to keep up with sea level rise (Kirwan and Megonigal 2013).

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References

Alauzet C, Jumas-Bilak E (2014) The phylum Deferribacteres and the genus Caldithrix. In: Rosenberg E, DeLong EF, Lory S, Stackebrandt E, Thompson F (eds) The Prokaryotes. Springer, Heidelberg, pp 595–611

Allison SD, Lu Y, Weihe C, Goulden ML, Martiny AC, Treseder KK, Martiny JB (2013) Microbial abundance and composition influence litter decomposition response to environmental change. Ecology 94: 714–725

Armstrong W, Cousins D, Armstrong J, Turner DW, Beckett PM (2000) Oxygen Distribution in wetland plant roots and permeability barriers to gas-exchange with the rhizosphere: a microelectrode and modelling study with phragmites Australis. Annals of Botany 86:687–703

Bertin C, Yang X, Weston LA (2003) The role of root exudates and alleloochemicals in the rhizosphere. Plant and Soil 256(1):67–83

Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW (2013) Historical reconstruction of mangrove expansion in the Gulf of Mexico: Linking climate change with carbon sequestration in coastal wetlands. Estuarine, Coastal and Shelf Science 119:7–16

Bokulich NA, Subramanian S, Faith JJ, Gever D, Gordon JI, Knight R et al (2013) Quality-filtering vastly improves diversity estimates from Illumina amplicon sequencing. Nature Methods 10:57–29

Brück WM, Sennett SH, Pomponi SA, Willenz P, McCarthy PJ (2008) Identification of the bacterial symbiont Entotheonella sp. in the mesohyl of the marine sponge Discodermia sp. The ISME Journal 2(3):335

Callaway RM, Thelen CC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427:731–733

Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK et al (2010a) QIIME allows analysis of high-throughput community sequencing data. Nature Methods 7(5): 335–336

Caporaso JG, Bittinger K, Bushman FD, DeSantis TZ, Anderson GL, Knight R (2010b) PyNAST: a flexible tool for aligning sequences to a template alignment. Bioinformatics 26(2):266–267

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W et al (2014) Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. PNAS 111:723–727

Chambers LG, Guevara R, Boyer JN, Troxler TG, Davis SE (2016) Effects of salinity and inundation on microbial community structure and function in a mangrove peat soil. Wetlands 36:361–371

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. Global Biogeochemical Cycles 17:1111

Coldren GA, Barreto CR, Wykoff DD, Morrissey E, Langley JA, Chapman SK (2016) Marsh grasses but not mangroves respond to chronic warming at the mangrove-marsh ecotone. Ecology. https://doi.org/10.1002/ecy.1539 Accepted Author Manuscript

Daims H, Lebedeva EV, Pjevac P, Han P, Herbold C, Albertsen M, …, Kirkegaard RH (2015) Complete nitrification by Nitrospira bacteria. Nature 528(7583):504

Donato D, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Markku K (2011) Mangroves among the most carbon-rich forests in the tropics. Nature Geoscience 4:293–297

Dos Santos HF, Cury JC, Do Carmo FL, Dos Santos AL, Tiedje J, Van Elsas JD, …, Peixoto RS (2011) Mangrove bacterial diversity and the impact of oil contamination revealed by pyrosequencing: bacterial proxies for oil pollution. PloS One 6(3):e16943

Doughty CD, Langley JA, Walker WC, Schaub R, Chapman SK (2016) Mangrove range expansion increases coastal wetland carbon storage. Estuaries and Coasts. https://doi.org/10.1007/s12237-015-9993-8

Edgar RC (2010) Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26(19):2460–2461

Fierer N, Allen AS, Schimel JP, Holden PA (2003) Controls on microbial CO2 production in surface and subsurface soil horizons. Global Change Biology 9:1322–1332

Freeman C, Ostle N, Kang H (2001) An enzymatic 'latch' on a global carbon store-a shortage of oxygen locks up carbon in peatlands by restraining a single enzyme. Nature 409:149

Giri C, Long J (2016) Is the geographic range of mangrove forests in the conterminous United States really expanding? Sensors 16(12):2010

Girnth AC, Grünke S, Lichtschlag A, Felden J, Knittel K, Wenzhöfer F, …, Boetius A (2011) A novel, mat-forming Thiomargarita population associated with a sulfidic fluid flow from a deep-sea mud volcano. Environmental Microbiology 13(2):495-505

Haouari O, Fardeau ML, Cayol JL, Fauque G, Casiot C, Elbaz-Poulichet F, …, Ollivier B (2008) Thermodesulfovibrio hydrogeniphilus sp. nov., a new thermophilic sulphate-reducing bacterium isolated from a Tunisian hot spring. Systematic and Applied Microbiology 31(1): 38-42

Heidelberg JF, Seshadri R, Haveman SA, Hemme CL, Paulsen IT, Kolonay JF, …, Daugherty SC (2004) The genome sequence of the anaerobic, sulfate-reducing bacterium Desulfovibrio vulgaris Hildenborough. Nature Biotechnology 22(5):554

Hongoh Y, Deevong P, Hattori S, Inoue T, Noda S, Noparatnaraporn N, …, Ohkuma M (2006) Phylogenetic diversity, localization, and cell morphologies of members of the candidate phylum TG3 and a subphylum in the phylum Fibrobacteres, recently discovered bacterial groups dominant in termite guts. Applied and Environmental Microbiology 72(10): 6780-6788

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant boil 1:274–287

Kandalepas D, Stevens KJ, Shaffer GP, Platt WJ (2010) How abundant are root-colonizing fungi in Southeastern Louisiana's degrades marshes? Wetlands 30(2):189–199

Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ (2016) Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. Global Change Biology 22:1097–1109

Kirwan ML, Megonigal JP (2013) Tidal wetland stability in the face of human impacts and sea-level rise. Nature 504:53–60

Krauss KW, From AS, Doyle TW, Doyle TJ, Barry MJ (2011) Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Thousand Islands region of Florida, USA. Journal of Coastal Conservation 15(4):629–638

Lipson DA, Raab TK, Parker M, Kelley ST, Brislawn CJ, Jansson J (2015) Changes in microbial communities along redox gradients in polygonized Arctic wet tundra soils. Environmental Microbiology Reports 7(4):649–657

Lücker S, Wagner M, Maixner F, Pelletier E, Koch H, Vacherie B, …, Daims H (2010) A Nitrospira metagenome illuminates the physiology and evolution of globally important nitrite-oxidizing bacteria. Proceedings of the National Academy of Sciences 107(30):13479-13484

McDonald D, Price MN, Goodrich J, Nawrocki EP, DeSantis TZ, Probst A et al (2012) An improved Greengenes taxonomy with explicit ranks for ecological and evolutionary analyses of bacteria and archaea. The ISME Journal 6(3):610–618

McKee KL, Mendelssohn IA, Hester MW (1988) Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of Rhizophora mangle and Avicennia germinans. American Journal of Botany 75(9):1352–1359

McLatchey GP, Reddy KR (1998) Regulation of organic matter decomposition and nutrient release in a wetland soil. Journal of Environmental Quality 27:1268

Mcleod E, Chmura GL, Bouillon S, Salm R, Bjork M, Duarte CM et al (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Frontiers in Ecology and the Environment 9:552–560

Methé BA, Nelson KE, Deming JW, Momen B, Melamud E, Zhang X, …, Brinkac LM (2005) The psychrophilic lifestyle as revealed by the genome sequence of Colwellia psychrerythraea 34H through genomic and proteomic analyses. Proceedings of the National Academy of Sciences of the United States of America 102(31):10913-10918

Meyer B, Kuehl J, Deutschbauer AM, Price MN, Arkin AP, Stahl DA (2013) Variation among Desulfovibrio species in electron transfer systems used for syntrophic growth. Journal of Bacteriology 195(5): 990–1004

Middleton BA, McKee KL (2001) Degradation of mangrove tissues and implications for peat formation in Belizean island forests. Journal of Ecology 89:818–828

Miroshnichenko ML, Kostrikina NA, Chernyh NA, Pimenov NV, Tourova TP, Antipov AN et al (2003) Caldithrix abyssi gen. nov., sp. nov., a nitrate-reducing, thermophilic, anaerobic bacterium isolated from a Mid-Atlantic Ridge hydrothermal vent, represents a novel bacterial lineage. International Journal of Systematic and Evolutionary Microbiology 53:323–329

Miroshnichenko ML, Kolganova TV, Spring S, Chernyh N, Bonch-Osmolovskaya EA (2010) Caldithrix palaeochoryensis sp. nov., a thermophilic, anaerobic, chemo-organotrophic bacterium from a geothermally heated sediment, and emended description of the genus Caldithrix. International Journal of Systematic and Evolutionary Microbiology 60(9):2120–2123

Morrissey EM, Franklin RB (2015a) Evolutionary history influences the salinity preference of bacterial taxa in wetland soils. Frontiers in Microbiology 6:1013

Morrissey EM, Franklin RB (2015b) Resource effects on denitrification are mediated by community composition in tidal freshwater wetlands soils. Environmental Microbiology 17(5):1520–1532

Morrissey EM, Gillespie JL, Morina JC, Franklin RB (2014) Salinity affects microbial activity and soil organic matter content in tidal wetlands. Global Change Biology 20:1351–1362

Nazina TN, Tourova TP, Poltaraus AB, Novikova EV, Grigoryan AA, Ivanova AE et al (2001) Taxonomic study of aerobic thermophilic bacilli: descriptions of Geobacillus subterraneus gen. nov., sp. nov. and Geobacillus uzenensis sp. nov. from petroleum reservoirs and transfer of Bacillus stearothermophilus, Bacillus thermocatenulatus, Bacillus thermoleovorans, Bacillus kaustophilus, Bacillus thermodenitrificans to Geobacillus as the new combinations G. stearothermophilus, G. th. International Journal of Systematic and Evolutionary Microbiology 51:433–446

Nellemann C, Corcoran E, Duarte CM, Valdes L, DeYoung C, Fonseca L et al (Eds) (2009) Blue carbon. A rapid response assessment. GRID-Arendal: United Nations Environment Programme. ISBN: 978-82-7701-060-1

Neubauer SC (2008) Contributions of mineral and organic components to tidal freshwater marsh accretion. Estuarine, Coastal and Shelf Science 78(1):78–88

Noll M, Matthies D, Frenzel P, Derakshani M, Liesack W (2005) Succession of bacterial community structure and diversity in a paddy soil oxygen gradient. Environmental Microbiology 7(3):382–395

Osland MJ, Enwright N, Day RH, Doyle TW (2013) Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. Global Change Biology 19(5):1482–1494

Perry CL, Mendelssohn IA (2009) Ecosystem effects of expanding populations of Avicennia germinans in a Louisiana salt marsh. Wetlands 28(1):396–406

Provancha MJ, Schmalzer PA, Hall CR (1986) Effects of the December 1983 and January 1985 freezing air temperatures on select aquatic poikilotherms and plant species of Merritt Island, Florida. Florida Scientist 49:199–212

Purnobasuki H, Suzuki M (2004) Aerenchyma formation and porosity in root of a mangrove plant, Sonneratia alba (Lythraceae). Journal of Plant Research 117:465–472

Raguenes G, Pignet P, Gauthier G, Peres A, Christen R, Rougeaux H, …, Guezennec J (1996) Description of a new polymer-secreting bacterium from a deep-sea hydrothermal vent, Alteromonas macleodii subsp. fijiensis, and preliminary characterization of the polymer. Applied and Environmental Microbiology 62(1):67–73

Rahman NA, Parks DH, Vanwonterghem I, Morrison M, Tyson GW, Hugenholtz P (2016) A phylogenomic analysis of the bacterial phylum Fibrobacteres. Frontiers in Microbiology. https://doi.org/10.3389/fmicb.2015.01469

Ransom-Jones E, Jones DL, McCarthy AJ, McDonald, JE (2012) The Fibrobacteres: an important phylum of cellulose-degrading bacteria. Microbial Ecology 63(2):267–281

Reddy KR, DeLaune RD (2008) Biogeochemistry of wetlands: science and applications. CRC Press, Boca Raton

Reddy KR, Rao PSC, Patrick WH (1980) Factors influencing oxygen consumption rates in flooded soils. Soil Science Society of America 44:741–744

Reed HE, Martiny JBH (2013) Microbial composition affects the functioning of estuarine sediments. The ISME Journal 7:868–879

Rietl AJ, Overlander ME, Nyman AJ, Jackson CR (2016) Microbial community composition and extracellular enzyme activities associated with *Juncus roemerianus* and *Spartina alterniflora* vegetated sediments in Louisiana saltmarshes. Microbial Ecology 71(2):290–303

Saarela M, Alakomi H, Suihko M, Maunuksela L, Raaska L, Mattila-Sandholm T (2004) Heterotrophic microorganisms in air and biofilm samples from Roman catacombs, with special emphasis on actinobacteria and fungi. International Biodeterioration & Biodegradation 54:27–37

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. Global Change Biology 20(1):147–157

Schimel JP, Schaeffer SM (2012) Microbial control over carbon cycling in soil. Frontiers in Microbiology 3:348

Schmidt EW, Obraztsova AY, Davidson SK, Faulkner DJ, Haygood MG (2000) Identification of the antifungal peptide-containing symbiont of the marine sponge Theonella swinhoei as a novel δ-proteobacterium,"Candidatus Entotheonella palauensis". Marine Biology 136(6):969–977

Schulz HN (2006) The Genus Thiomargarita. In: Dworkin M, Falkow S, Rosenberg E, Schleifer KH, Stackebrandt E (eds) The Prokaryotes. Springer, New York, pp 1156–1163

Simpson LT, Feller IC, Chapman SK (2013) Effects of competition and nutrient enrichment on Avicennia germinans in the salt marsh-mangrove ecotone. Aquatic Botany 104:55–59

Skelton NJ, Allaway WG (1996) Oxygen and pressure changes measured in situ during flooding in roots of the Grey Mangrove Avicennia marina (Forssk.) Vierh. Aquatic Botany 54(2–3):165–175

Slobodkin AI, Tourova TP, Kostrikina NA, Chernyh NA, Bonch-Osmolovskaya EA, Jeanthon C, Jones BE (2003) Tepidibacterthalassicus gen. nov., sp. nov., a novel moderately thermophilic, anaerobic, fermentative bacterium from a deep-sea hydrothermal vent. International Journal of Systematic and Evolutionary Microbiology 53(4):1131–1134

Smith KA (1987) An overview of the Indian River Lagoon. University of Florida, Florida

Sonne-Hansen J, Ahring BK (1999) Thermodesulfobacterium hveragerdense sp. nov., and Thermodesulfovibrio islandicus sp. nov., two thermophilic sulfate reducing bacteria isolated from a Icelandic hot spring. Systematic and Applied Microbiology 22(4):559–564

Sorrell BK, Armstrong W (1994) On the difficulties of measuring oxygen release by root systems of wetland plants. Journal of Ecology 82:177–183

Strickland MS, Lauber C, Fierer N, Bradford MA (2009) Testing the functional significance of microbial community composition. Ecology 90:441–451

Tan HQ, Wu XY, Zhang XQ, Wu M, Zhu XF (2012) Tepidibacter mesophilus sp. nov., a mesophilic fermentative anaerobe isolated from soil polluted by crude oil, and emended description of the genus Tepidibacter. International Journal of Systematic and Evolutionary Microbiology 62(1):66–70

Urios L, Cueff V, Pignet P, Barbier G (2004) Tepidibacter formicigenes sp. nov., a novel spore-forming bacterium isolated from a Mid-Atlantic Ridge hydrothermal vent. International Journal of Systematic and Evolutionary Microbiology 54(2):439–443

Wang Q, Garrity GM, Tiedje JM, Cole JR (2007) Naïve Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Applied and Environmental Microbiology 73(16):5261–5267

Ward NL, Challacombe JF, Janssen PH, Henrissat B, Coutinho PM, Wu M et al (2009) Three genomes from the phylum acidobacteria provide insight into the lifestyles of these microorganisms in soils. Applied and Environmental Microbiology 75:2046–2056

Wolf AA, Drake BG, Erickson JE, Megonigal JP (2007) An oxygen-mediated positive feedback between elevated carbon dioxide and soil organic matter decomposition in a simulated anaerobic wetland. Global Change Biology 13:2036–2044

Wu YM, Yang J, Fan XL, Fu SF, Sun MT, Guo RB (2017) Elimination of methane in exhaust gas from biogas upgrading process by immobilized methane-oxidizing bacteria. Bioresource Technology 231:124–128

Yando ES, Osland MJ, Willis JM, Day RH, Krauss KW, Hester MW (2016) Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. Journal of Ecology 104(4): 1020–1031

Yarwood S, Brewer E, Yarwood R, Lajtha K, Myrold D (2013) Soil microbe active community composition and capability of responding to litter addition after 12 years of no inputs. Applied and Environmental Microbiology 79:1385–1392